**High pollinator population connectivity in heavily disturbed landscapes: substantial gene flow despite large urbanized areas in two hoverflies**

Julian Wittische 1,2,\*, Ximo Mengual 3, Frank Drygala, Joerg Mehnert, Hinatea Ariey1,2, Stéphanie Lippert1,2, Amanda Luttringer1,2, Alain Frantz 1,2

Provisional/add relevant authors

1: Musée National d’Histoire Naturelle, 25, rue Muenster, L-2160, Luxembourg, Luxembourg

2: Fondation Faune-Flore, 24, rue Muenster, L-2160, Luxembourg, Luxembourg

3: Zoologisches Forschungsmuseum Alexander Koenig, Leibniz‐Institut zur Analyse des Biodiversitätswandels, Adenauerallee127, D‐53113 Bonn, Germany

\*: Corresponding author (julian.wittische@mnhn.lu)

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**ABSTRACT**

Hoverflies (Syrphidae) are essential pollinators, and their severe decline jeopardizes their enormous contribution to plant diversity and agricultural production. However, we know little about the dispersal abilities of hoverflies in urbanized landscapes, limiting our understanding of the spatiotemporal dynamics of plant–pollinator systems, and reducing our ability to preserve biodiversity in the context of global changes. Previous work has not addressed how urbanization affects the functional connectivity of hoverflies, and whether dispersal is a limiting factor in their population dynamics. In this study, we investigate the spatial genetic structure and spatial variation in genetic diversity of two species of hoverflies in two urban areas. Using thousands of specimens collected by hand netting from two western Europe urbanized study areas of 490 km2 and 460 km2 in 2021, we identified XX and 24 microsatellite SNP loci for *Syritta pipiens* and *Myathropa florea*, respectively. Using STRUCTURE, DAPC and IBD analyses, we found evidence for high genetic connectivity for both species, suggesting effective dispersal at scales larger than metropoles, despite urbanization. Although anthropogenic land cover changes generally have dramatic consequences on biodiversity, some hoverfly species retain high connectivity, which suggests that dispersal is not a strong limiting factor in their metapopulational dynamics. Provided we maintain or restore habitat, recolonization should therefore be prompt even in urban areas.

**KEYWORDS**

Landscape genetics; Spatial ecology; Diptera; Urbanization; Machine learning

# INTRODUCTION

Pollinators provide a key ecosystem service to agricultural crops and wild plants, but they are declining across the world. It has been estimated that, globally, the economic value of pollination is worth hundreds of billions of US dollars (Doyle et al., 2020; Gallai et al., 2009). The vast majority of crops (Klein et al., 2007; Reilly et al., 2020) and of wildflowers (Ollerton et al., 2011) benefit from insect pollination by, in particular, bees and hoverflies (Potts et al., 2015). Pollinators also support an immense range of other organisms (Ollerton, 2017). However, evidence of the loss of pollinators is clear-cut: wild pollinators are declining at local, regional and global scales, in both diversity and abundance (Biesmeijer et al., 2006; Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2021, 2019; Senapathi et al., 2015). The main underlying drivers behind declines are the intensification of land-use, climate change, and the spread of invasive species and parasites/pathogens (Dicks et al., 2021; Ollerton, 2017; Potts et al., 2010; Vanbergen et al., 2013). The spread of urban areas and the intensification of agriculture have resulted in the destruction and fragmentation of many of pollinator habitats (Seibold et al., 2019). There is still a considerable lack of knowledge on the mechanisms underlying the responses of invertebrate pollinators to fragmentation resulting from land-use change (Dicks et al., 2013; Gill et al., 2016; Simmons et al., 2019; Winfree et al., 2011).

Because of demographic growth, land use change for new infrastructure and urban development is expected to be considerable even in already heavily urbanized countries. This, in turn, will lead to further loss and fragmentation of natural and semi-natural habitats (Jaeger et al., 2016). Cologne is the fourth-most populous city in Germany and recently commissioned a major inventory of pollinators (Stadt Köln, 2022), notably stimulated recent findings about country-wide insect declines (Hallmann et al., 2017; Seibold et al., 2019). Luxembourg has recognized that habitat loss and fragmentation are threatening its biodiversity in general and insect pollinators in particular (Ministère de l’Environnement, du Climat et du Développement durable, 2022). Key strategies to counteract the negative effects of habitat fragmentation include the design of a network of ecological corridors as well as land set-a-side to support pollinators within the agricultural landscape. In order for these mitigating measures to be successful, however, it is important to understand the functional connectivity of the landscape from the viewpoint of the pollinator (Dreier et al., 2014; Rands, 2014).

Although dispersal is a key trait to deal with habitat fragmentation, we only have a limited understanding of dispersal for most insect pollinators.Dispersal is required to maintain connectivity in the face of landscape fragmentation, to colonize new habitats and to allow re-colonization after local extinction. Dispersal therefore impacts species distribution, community structure, (meta-)population dynamics, gene flow and extinction risk (Bowler and Benton, 2005). Species with high dispersal ability generally are better able to move efficiently between suitable habitat patches and may exploit fragmented resources more efficiently (Öckinger et al., 2010). Nevertheless, the results from work on Apiformes suggest that even good dispersers can be impacted by habitat fragmentation. Bumblebee (Bombus) species normally exhibit very little genetic structure (Dreier et al., 2014; Lozier et al., 2011). However, impervious cover associated with built-up areas significantly limited gene flow in a North American bumblebee (Jha and Kremen, 2013). Even at larger spatial scales, urban areas can be a substantial gene flow barrier for pollinators (Davis et al., 2010). A particular difficulty with evaluating the impact of land-use change relates to the fact that flying ability and response to habitat fragmentation differs significantly between pollinators, even between closely related (Greenleaf et al., 2007; Jauker et al., 2009; Steffan-Dewenter et al., 2002). We thus need to better understand the effect of landscape disturbance on the connectivity of pollinators (Taylor et al., 1993), the geographic scale at which mitigation measures should be implemented, and which element of the population dynamics of pollinators is the most sensitive to anthropogenic disturbance.

Hoverflies (Syrphidae) are an important group of pollinators, but they are understudied relative to bees, and little is known about their dispersal and their response to landscape fragmentation. Hoverflies are a biologically very diverse family of flower-visiting flies (Bickel et al., 2009; Speight, 2017; Wardhaugh, 2015). Their dependence on floral resources makes hoverflies the most important pollinators besides bees, providing a major contribution to plant diversity and agricultural production (Hodgkiss et al., 2018; Jauker et al., 2009; Pekas et al., 2020; Rader et al., 2016; Ssymank et al., 2008). Species do not display strict selectivity for specific flower species (Branquart and Hemptinne, 2000; Lucas et al., 2018) which make them especially important in disturbed landscapes (Jauker et al., 2009). Many hoverfly larvae feed on aphids and are effective biocontrol agents, especially in agricultural landscapes (Pekas et al., 2020; Speight, 2017), which adds to their large contribution to human food security. Hoverflies usually move a few hundred meters and tall vegetation and bare soil including ploughed fields and roads can act as barriers (Lövei et al., 1998; Wratten et al., 2003). Similarly, studies investigating hoverfly richness in relation to habitat patch isolation suggest that hoverflies are significantly impacted by habitat fragmentation (Jauker et al., 2019; Moquet et al., 2018; Ouin et al., 2006). However, other studies have highlighted the high dispersal ability of hoverfly species. Some individuals are able to cover more than 100 km in less than 3 days during migration (Aubert et al., 1969; Aubert and Goeldlin de Tiefenau, 1981), and potentially more than a thousand kilometer over the whole migration season (Jia et al., 2022; Ouin et al., 2011), especially when aided by wind (Gao et al., 2020; Wotton et al., 2019). Given the high prevalence of hoverfly species presenting a partial migration syndrome (Doyle et al., 2022; Menz et al., 2019; Speight, 2017), the genetic and structural pathways to efficient dispersal might also be present in non-migratory hoverflies. Indeed, even rare non-migratory species may fly several kilometers away from their emergence sites (Rotheray et al., 2014).

Molecular genetic methods are powerful tools to investigate the effect of fragmentation on target species where dispersal capability is hard to evaluate directly, but such methods have seldom been used on hoverflies. Capture-mark-recapture (CMR) methods have been used to study hoverfly dispersal in the past (Aubert et al., 1969; Aubert and Goeldlin de Tiefenau, 1981; Rotheray et al., 2014). However, given the limitations of conducting CMR across a large area for abundant small insects, landscape connectivity is easier to investigate using molecular genetic methods. Genetic connectivity is evaluated through a quantification of gene flow, which is directly related to dispersal as genes are propagated by individuals or propagules which disperse before reproduction (Broquet and Petit, 2009; Cayuela et al., 2018). Therefore, the greater the genetic connectivity is, the easier it is to disperse through the landscape. One population genetics hoverfly study described continental-scale patterns for migratory species (Raymond et al., 2013) for which one expect no strong isolation-by-distance or landscape resistance signal at a regional scale, due to the extreme genetic mixing associated with mass migration. Another hoverfly study found no substantial barriers to gene flow, though they used a small number of individuals, from a fraction of a low disturbance forest landscape (Schauer et al., 2018). However, the effect of urbanization on hoverfly functional connectivity has, to our knowledge, never been studied.

In this study, we investigate the genetic diversity, structure, and isolation-by-distance of two species of hoverflies, *S. pipiens* and *M. florea*, based onthousands of individuals in two urbanized landscapes in Western Europe.We expect some genetic structure and IBD at the landscape scale due to the large extent and the anthropogenic nature of the study areas, notably the large unvegetated impervious areas present in and around cities.

# METHODS

## | Study areas, study organisms, and sampling

Study areas

The shape of the Luxembourg study area was chosen to focus on the two largest urban agglomerations in the country Luxembourg and Esch-sur-Alzette.

As study organisms, we chose *Syritta pipiens* (Linnaeus, 1758) and *Myathropa florea* (Linnaeus, 1758), two hoverfly species with long flight seasons and likely to occur across the whole study areas based on known preferred habitats preliminary field experience and previous inventories. We avoided migratory species because there genetic variation is less likely to bear signal of isolation by distance and structure (Raymond et al., 2013) given their sometimes massive ability to spread (Jia et al., 2022). Our sampling design was to catch at least 1 individual per squared kilometer in order to have as few gaps in geographical coverage as possible, following a uniform grid. The analytical purpose of this sampling design was to decrease bias and improve our accuracy in detect influential landscape features, if there were any (Oyler-McCance et al., 2013; Schwartz and McKelvey, 2009). We caught 831 and 1226 *S. pipiens* individuals, and 559 and 394 *M. florea* individuals in Cologne and the Luxembourg study area, respectively (Fig. X).

## | Laboratory procedures

MENTION WE CHECKED OUTLIERS AND THEY CAME BACK AS OUR TARGET SPECIES

## | Genetic diversity

We conducted all analyses in this manuscript in R (R Core Team, 2022) using RStudio (RStudio Team, 2022), except for the STRUCTURE analysis.

We conducted basic analyses of our genetic datasets using the *adegenet* v. 2.1.7 (Jombart, 2008; Jombart and Ahmed, 2011) ,the *hierfstat* v.0.5.11 (Goudet, 2005), the *pegas* v. 1.1 (Paradis, 2010), the *PopGenReport* v. 3.0.7 (Adamack and Gruber, 2014) and the *poppr* v. 2.9.3 (Kamvar et al., 2014) R packages. We evaluated allelic richness, heterozygote deficiency, overall fixation indices with bootstrap confidence interval, fixations indices per locus, and the pairwise genetic distance between our study areas. To explore linkage disequilibrium in our dataset, we also calculated standardized indices of association over all loci with a one-sided permutation test, as well as pairwise indices among all loci (Agapow and Burt, 2001; Kamvar et al., 2014). We also evaluated whether null alleles were likely using two resampling-based tests (Brookfield, 1996; Chakraborty et al., 1994). Prior to running genetic structure analyses, we decided to remove only loci which presented both linkage disequilibrium and extreme heterozygote deficiency, as well as a frequency of null alleles at a locus significantly different from zero. Therefore, we remove one locus from the *S. pipiens* dataset (Spp141).

## | Clustering and isolation-by-distance

We used two different approaches to estimate the most likely number of distinct genetic clusters (K). First, we considered a Bayesian model-based approach and used STRUCTURE v. 2.3.4 (Pritchard et al., 2000), and chose the admixture model and correlated allele frequencies. An important parameter to set it α, the Dirichlet prior parameter for the degree of admixture (Hubisz et al., 2009) which conceptually represents the number of ancestral populations from which each individual’s alleles originate. We set the inference of a different α for each study area and allowed unequal representation of source populations in the sample (alternative ancestry prior). We also set initial values of α it to 1/K because this parametrization led to lower average assignment errors in a simulation study (Wang, 2017). We conducted ten independent runs with 200 000 Markov Chain Monte Carlo burn-in iterations followed by 1 000 000 iterations for one to five clusters. We ruled out higher numbers of cluster based on preliminary analyses. To determine the most likely number of clusters, we directly compared log-likelihoods for all K values across the ten runs, and we used the ΔK statistic which is based on the rate of change in the log probability of data given K (Evanno et al., 2005). We also surveyed the variation in STRUCTURE outputs and matched clusters across runs to avoid issues with label change and multimodality. DISPLAY AVERAGE OR BEST RUN?

Secondly, we considered a model-free approach which is less reliant on assumptions and used discriminant analysis of principal components (DAPC; Jombart et al., 2010, 2009). We considered both a grouping prior based on study areas (2 study areas = 2 potential clusters) and *de novo* grouping because several studies have highlighted that those two alternatives may produce different clustering outcomes (Glück et al., 2022; Miller et al., 2020). When no grouping is input (*de novo*), DAPC uses sequential k-means to find potential clusters prior to the estimation of the best number of genetic clusters. We followed the up-to-date recommendations from the development team regarding the appropriate steps to conduct DAPC (Jombart and Collins, 2022). When using the *de* novo method, we first conducted a principal components analysis which transforms the genotype data to a new coordinate system and generates linear combinations of genetic information. Each of those combinations, also called components or eigenvectors, aligns with the direction of maximum variance in the rotated data while being orthogonal to the previous component. Using all the principal components, we then ran k-means with 1000000 iterations and used Bayesian Information Criterion (BIC) to evaluate the performance of K values from 1 to 20. We chose the K represented by a BIC presenting an elbow in the curve of BIC values as a function of k. This is similar to the moment interpretation of likelihood values for STRUCTURE. Regardless of the method we used to describe potential clusters, we chose the best number of components to retain for the DAPC based on both cross-validation and *a*-score optimization. This is a necessary step because the first few components represent most of the genetic variation, we want to find a balance to preserve discrimination power while avoiding overfitting. We also conducted 1000 *de novo* runs with different seeds and 1000000 k-means iterations to evaluate whether they converged on the same number of clusters, and when they converged whether they produced similar clusters. We systematically used all discriminant functions for the assignment of individuals into clusters and used cross-validation to evaluate the general performance of the DAPC and compared it with a random classifier.

To explore whether isolation-by-distance (IBD) is responsible for genetic differentiation in our study landscapes, we first evaluated the linear relationship between the natural logarithms of geographic distance and Loiselle’s kinship values (Loiselle et al., 1995) which measure the genetic relatedness between pairs of individuals. The usual increasing pattern of IBD is, of course, expected to be decreasing one given that kinship is a similarity metric rather than a distance/dissimilarity metric. We chose this genetic distance because it is considered a less biased estimator with low sampling variance (Vekemans and Hardy, 2004). We also computed Mantel’s permutation test for similarity of our two distance matrices (1-Loiselle’s kinship and geographic distance). Finally, to understand the scale at which genetic structure is shaped by dispersal we created a Mantel correlogram using Sturge’s rule to define distance classes and used a Monte Carlo procedure to test whether correlation values are significant.

Because IBD was so low for both species – slopes were not significantly different from 0 within study areas – we could not investigate isolation-by-resistance and the landscape genetics of those two species as was originally planned (Peterman, comm. pers 2022).

# RESULTS

## | Genotyping and filtering

## | Genetic diversity

High Fis, low Fst. Allelic richness increase with sample size. Slight differentiation between study areas. Meh diversity.

## | Clustering and isolation-by-distance

K=2 but very messy, so really K=1?

No IBD within study areas.

# DISCUSSION

## | High large-scale population connectivity but low genetic diversity

Our study showed that two species of hoverflies present high genetic connectivity across tens of kilometers of urbanized landscapes bearing natural and artificial barriers.

Other studies.

Our positive results about the genetic connectivity should nevertheless be contrasted to the low genetic diversity in both species. Although our study species were widespread and abundant according to our sampling teams, their low genetic diversity could limit resilience when facing catastrophic events or gradual environmental changes. Indeed, genetic diversity is the raw material for evolutionary adaptation necessary to overcome environmental constraints on survival and growth. The hoverfly populations we studied could be at risk such as a new disease, or the ongoing threat of climate change. which may affect the sequential use of flower by the hoverfly community throughout the season by affecting plant phenology.

## | Implications for hoverfly biodiversity and pollination services

Although we did not find Constraints on gene flow within urbanized landscapes, they are likely to exist in other systems.

Reminder of threats and how dispersal and connectivity could be used to help understand and mitigate declines.

Highlighting that, given proper habitats, hoverfly could quickly colonize the landscape and that habitat quality and quantity are likely more limiting that isolation between habitat patches. Wildflower strips distributed homogenously in an agricultural or urban landscapes could support some hoverfly species and would foster their pollinator services and their large contribution to aphid control. For some species, urban centers could act as a refuge when the surrounding landscape is unfavorable due to heavy pesticide use or lack of floral resources. Some cities may carry … (car net papers, Cologne hoverfly inventory paper).

Some introduced hoverflies can potentially outcompete native species due to their high polyphagy and dispersal abilities. The high effective dispersal ability of *M. florea* suggested in our study suggests that thissin our study suggests that tho. species can live in and move through disturbed habitats in Europe. *M. florea* has been introduced on the west coast of North America pre-2005 (BugGuide, 2022), likely through the timber trade because their larvae often develop among decaying roots or in rot-holes of trees, or with associated decaying matter (Rotheray, 1993). Unfortunately, *M. florea* has already spread from on the east coast of North America (GBIF.org, 2022; Miranda et al., 2013). *M. florea* were seen feeding on more than 10 species of flowers during the fieldwork for this study (Wittische, unpublished); many hoverflies are known to be highly polyphagous (Branquart and Hemptinne, 2000). Furthermore, given a similar climatic niche, widespread larval habitat, high dispersal ability and its tolerance for disturbance and urbanization suggested by our study, we expect *M. florea* to spread further East in North America. *Merodon equestris* is a European species now present in East Asia, North America, and Oceania (Hong et al., 2012; Thompson, 2008) and is a major pest of daffodils.. *Eristalis tenax*, another European species, is a strong competitor due to its polyphagy, strong dispersal and aggressive territorial behavior towards other pollinators (Wellington and Fitzpatrick, 1981). *E. tenax* has spread through North America and New Zealand where they reach high abundances. Finally, *Simosyrphus grandicornis* is an Australasian species which has been introduced to Hawaii and French Polynesia where no previous hoverfly species occurred (Doyle et al., 2020), which may have affected the floral and pollinator communities. The lack of knowledge about hoverfly introductions and their potential consequences on biodiversity is dire and further highlight why it is crucial to understand hoverfly dispersal and their population dynamics.

## | Methodological limits and future directions

We could not do fancy landscape genetics model, however there might still be effects of the landscape on movement and on population health.

Although STRUCTURE may perform better than DAPC in some scenarios because DAPC may be sensitive to IBD, DAPC performs well for scenarios with low IBD (Blair et al., 2012) which was the case in our study.

We have started investigating genetic connectivity for other pollinators which may be more sensitive to anthropogenic landscape disturbance in one of our study areas (Luxembourg). They include a bee fly (*Bombylius major*), which is dependent on wild bee hosts and may be limited in its effective dispersal by the same landscape features affecting its hosts, and a wild bee (*Andrena cineraria*). Distance to suitable habitat is known to limit wild bees use of the landscape relative to hoverflies so it will be interesting to compare their results to those of this study. Finally Microsatellite vs. SNPs for genetic structure/IBD/IBR. Mention IBE. A number of statistical tools using next generation whole-genome sequencing data have recently been developed.

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